Simulating social network evolution in cooperatively breeding animals using agent-based models

Undergraduate research thesis

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by

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Abstract

Individuals of a social group can only benefit from group living if the group structure is maintained and conflicts are managed. Dominance hierarchies can help groups to manage conflict by reducing the number of aggressive encounters. This research explores the effects of winner-loser effect, search radius and number of territories on the connectedness, cohesion and linearity of the network structure. Results indicates that presence of winner-loser effect and long search radius allow individuals to have more interactions with other members of the group, forming strong dominance hierarchies with high connectedness, high cohesion and a more linear hierarchy. Number of territories was shown to have no significant effect on the network structure possibly due to the failure of the territory to function as focal location for interaction. The study of the emergence of network structure can provide insights to the evolution of social groups.

Introduction

Social interactions among individuals of a social group create a network structure. The maintenance of a stable group structure is important to social species since group living provide numerous benefits to individuals of the group. Living with conspecifics allow individuals to recruit help from other members of the group, increasing their inclusive fitness (Wong & Balshine, 2011). Other benefits of group living include lower risk of predation (Beauchamp, 2014), access to mates (Baglione, Marcos, Canestrari, & Ekman, 2002) and reproductive division of labor (Rypstra, 1993). Group living also comes at a cost. Reproductive and food competition among individuals of a social group can be higher than that of solitary individuals (Schradin, König & Pillay, 2010). Individuals of a social group face high competition for resources, leading to aggressive interactions between individuals (West-Eberhard, 1979). Inbreeding risk is also higher for individuals living in groups, resulting in higher offspring mortality (Godoy, Vigilant, & Perry, 2016). Costs and benefits of group living can differ among members of the group, sparking conflict of interest.

To promote group cohesion, individuals of a social group have to place the needs of the group above individual needs at times (Sueur & Maire, 2014). When such compromises are not met, conflict of interest for resources or mates can occur, resulting in eviction (Sueur, Deneubourg, Petit & Couzin, 2011). Eviction is costly to both the evicted individual and the other group members. Evicted individuals are often chased away from the group and forced to survive in distant and unfamiliar environments, resulting in a low survival rate (Stephens, Russell, Young, Sutherland, & Clutton-Brock, 2005). Reduction in group size after eviction increases the workload of breeders and reduces the survival rate of the group, for example, since the smaller groups have a lesser chance of detecting predators (Clutton-Brock *et al*., 1999). Because of such costs to individuals, natural selection can favor the evolution mechanisms of conflict management to avoid or reduce the occurrence of conflicts and promote group cohesion.

Formation of a dominance hierarchy, where individuals remember the results of previous interactions and behave according to their dominance status (West-Eberhard, 1979), can help manage conflict in groups. A dominance hierarchy is a group structure in which individuals are ranked relative to one another based on pairwise aggressive interactions. Relatively dominant individuals are ranked at the top of the hierarchy whereas relatively submissive individuals are ranked at the bottom. By having a clear ranking system, individuals can reduce the number of aggressive encounters, thereby reducing the cost of fighting, benefitting themselves as well as social partners (Moosa & Ud-Dean, 2011). A clear hierarchy allows a pair to have an accurate prediction of the aggressive encounter result based on their relative dominance. Being aware of the predicted results will spare the pair the need to determine the winner through a fight, therefore reducing the number of costly aggressive encounters for both members of the pair. In some systems (e.g., social wasps, Thompson et al. 2014), information about dominance values can be forgotten in the absence of fights. Maintenance of the dominance hierarchy can require regular interactions between individuals of the social group.

Dominance hierarchies develop from the outcome of interactions among group members. The outcome of fights can be purely based on size and the ability to control resources. Alternatively, the outcome of fights can be influenced by past experiences. In some species, winning increases the probability of winning future interactions (winner effect) and losing a fight decreases the probability of winning future interactions (loser effect) (Schwartzer, Ricci & Melloni, 2013). Winners of previous fights reduce the length of fight time in future encounters, saving them time and energy. On the other hand, losers of previous fights receive less aggression during the following aggressive encounters, minimizing the chance of injury (Lehner, Rutte, & Taborsky, 2011). Winner-loser effects are important in the formation of dominance hierarchies since it facilitates the establishment of a more linear hierarchy (Goessmann, Hemelrijk, & Huber, 2000).

This paper aims to study the emergence of structure of social networks in response to conflict. A multi-agent modeling program, NetLogo (Wilensky, 1999), was used to simulate social network structures. The general structure of the model was based on group-living fish such as the cooperatively breeding cichlid fish, *Neolamprologus pulcher*. These fish form dominance hierarchies based on size, in which the largest male and female in a group are genetic parents to most of the offspring (Wong, & Balshine, 2011). However, the model was not parameterized for any particular system.

This research explored the hypothesis that the interactions responsible for the emergence of strong dominance hierarchies are associated with group cohesiveness and group structure. To do so, I tested the effects of the presence of winner-loser effects and the location of interactions on the formation of hierarchies and on group cohesiveness, connectivity, and structure. Winner-loser effects are predicted to result in linear hierarchies as suggested by other authors (Lehner, Rutte, & Taborsky, 2011). Therefore, I predict that incorporating winner-loser effects should lead to more linear hierarchies, more cohesion and less modularity, giving rise to high connectivity within strong dominance hierarchies. Groups with a strong dominance structure are predicted to have high centralization values (a measure of variation in connectivity) because some individuals are more influential on network connectivity than others, although which individuals are influential may depend on the measure of connectivity. Higher number of territories, which allow for an increase in the number of focal locations for interactions is predicted to result in a higher number of communities, lower group cohesion, lower connectivity and a less linear hierarchy. I also predict that an increase in search radius should increase the number of possible interactions due to an increased range of interaction, leading to higher connectivity, cohesion and a more linear dominance hierarchy.

Methods

Descriptions of the agent-based model used in this section follows Grimm's ODD (Overview, Design concepts, and Detail) protocol (Grimm *et al*., 2010).

Purpose

The dynamics of aggressive social networks were simulated using a multi-agent modeling program, NetLogo. The model was inspired by behavioral patterns observed in studies of *Neolamprologus pulcher*, but the model does not include data from real-world experiments.

Agents

Two types of agents, territories and individual fish, are present in the model. Territories are the locations that tend to attract individuals, and are inspired by breeding shelters on *N. pulcher* territories.

State variables

State variables refer to the physical and biological characteristics of an agent (Grimm *et al*., 2010). Both the agents and the environment possess state variables. Table 1 and Table 2 list the state variables of agents and environments respectively.

Scales

The time scale for each run is set at 100 steps arbitrary units. However, aggression data is only collected after 80 steps to reflect real life observations during an experiment. Conflicts take place constantly throughout a fish's lifetime. However, when researchers collect their observation data, only events during the specific time frame of the observation can be captured.

Coordinates of the world are set at 32 × 32 arbitrary units. The world wraps around both horizontally and vertically. Individuals leaving from the top will appear at the bottom and vice versa. Similarly, individuals leaving from the left will appear at the right and vice versa.

Design concepts

I. Basic principles

This model was inspired by the interactions in dominance structured groups of fish. In these fish, such as *Neolamprologus pulcher*, dominance level is closely related to size. Aggression tends to be directed from larger, more dominant individuals to smaller, subordinate individuals, but restricted to individuals that are similar in rank. For example, individuals are most aggressive towards a slightly smaller individual compared to itself. Large individuals tend to spend time near breeding shelters (territories). Losers of fights often move away from breeding shelters, at least temporarily.

II. Emergence

Key emergent phenomenon in this model are the directed, weighted links that describe the frequency of aggressive encounters from the aggressor to the recipient during time steps 80-100.

III. Adaptation

Winners of a fight and individuals with high dominance value will move toward territories. Individuals who were not successful at a fight will move away from territories.

IV. Objective

Individuals do not act to increase an objective. Although wining fights have fitness consequences, fitness maximization was not incorporated into the model.

V. Learning

Agents do not learn.

VI. Prediction

Agents do not predict the future state of the system

VII. Sensing

Agents sense other agents and territories within their search radius.

VIII. Interaction

Individuals pick a target based on similar rank and initiate fights, in which the relatively more dominant individual always wins.

IX. Stochasticity

Initial placement of individuals on the map is random; the decision for more dominant individuals to move to a nearby territory, and selection of a target are partly random.

X. Collectives

Individuals belong to a social network.

XI. Observation

At tick 80, weighted, directed link between each pair of individuals are formed and recorded. At tick 100, the links are reported in the output.

Initialization

Initialization refers to the initial conditions of the model world for each run. I ran simulations using a full factorial design for the values shown in Table 3. However, results are only described for runs of 15 individuals per sex.

Process overview and scheduling

The flow of steps in the model is described in this section, together with the conditions for each step.

After initializing the model based on the specified number of individuals, territories, selecting the type of aggression and whether the dominance values are fixed for the run, the "go" step calls the "move" and "aggression towards similar rank" submodels (see below), in that order, before moving on to the next time step.

Both types of aggression procedure will allow individuals to have a chance to pick a target based on specified criteria. After the selection of a target, the "fight" submodel is initiated. During time steps 80-100, directed links from aggressor to target are created. Each aggressive action from one individual to another increases the weight of the link by 1.

Submodels

Submodels refer to the detailed process happening in each step.

The "setup" submodel involves creating the initial number of males, females and territories specified. The "go" submodel calls for "move" and "aggression towards similar rank" during each time step ("tick"). During each tick, every fish has a tendency of changing its dominance value toward an intermediate dominance value of 50. The dominance value is altered by $D + 0.2 \times (50 - D)$, where D is the current dominance value. This equation will cause individuals with dominance values that deviate from a value of 50 to tend to revert toward a value of 50. Resetting the dominance value back to an intermediate value reflects the tendency of individuals to forget past conflicts. If ‘fixed dominance’ is set to ‘yes’, dominance values do not change.

During “move”, each individual makes a turn towards the left at a random angle of between 0˚ to 90˚, followed by a turn towards the right at a random angle of between 0˚ to 90˚ and one step forward. For individuals with dominance value of higher than 40, there is an 80% chance that they will take one step towards a territory if there is one within its search radius. Since dominant fish are more territorial than less dominant fish, a more dominant individual will have a higher probability of seeking out a territory and occupying it.

When “aggression towards similar rank” is called forth, individuals randomly choose a target within their search radius. The probability that individual *i* is aggressive to a target will be $q = f_{ir}(-0.02 \times C + 1)$, where C represents the absolute value of the difference in dominance value between the individual and its target and r is the rank of the target. When the dominance difference between individual *i* and its target approaches 0, q approaches 1.
Once a target is chosen, both modes of aggression will have 0.9 probability of fight occurrence if the chosen target is of the same sex as individual *i*. If the target is not of the same sex, the probability of a fight is 0.1.

During a fight, the more dominant individual of the pair will be the aggressor while the less dominant individual will be the recipient. The aggressor will increase its dominance value by 10 and take one step towards a nearby territory if there is one within its search radius. Dominance value of the recipient will decrease by 10 and it will take 4 steps away from a territory if there is one within its search radius. Since territories are limited, they will only be claimed by the more dominant individuals of a social group. The aggressor will form a directed link to the target, representing the direction of aggression. Every link starts off with a weight value of one. Subsequent aggression between the same pair will increase the link weight by one each time a fight takes place in the same direction.

If the model is running under fixed dominance, neither the winner's nor the loser's dominance value changes during a fight, but the link will still be formed.

Data collection and analysis

Data was collected by running behavioral space analysis after the model is built using NetLogo 6.0.2 in a full factorial design, varying the variables across values described in Table 3. R (R Core Team 2014) package, igraph, is used to construct a network for each run. Mean betweenness centrality, mean closeness centrality, mean indegree, mean outdegree, mean eigenvector centrality of each node was calculated. Betweenness centrality is the number of shortest paths going through a node. Closeness centrality measures degree to which an individual is near all other individuals in a network. Indegree measures the count of links directed to the node, while outdegree measure the count of links directed away from the node. Eigenvector centrality measures the influence of a node in a network. For each of these centrality measures, I calculated centralization. Centralization measures measure the extent to which the network is structured. If individuals are connected evenly, centralization value will be low. If some individuals are more central to the network compared to the others, centralization value will be high.

I also calculated linearity, cohesion, modularity and number of communities from each network generated. A characteristic of a strong dominance hierarchy is having high linearity (De Vries, 1995). Linearity is a measure of how transitive relationships in the dominance hierarchy are. Triads with a linear hierarchy are referred to as transitive (A dominates B, B dominates C, A dominates C) whereas non-linear triads are intransitive (A dominates B, B dominates C, C dominates A). For networks with high linearity, more transitive triads are expected to be present, with few or no intransitive triads. I used Landau's h (De Vries, 1995) as a measure of linearity.

There are several ways to measure cohesiveness. "Cohesion" refers to the minimum number of links to be broken to separate one node from the network structure (Abell et al., 2013). A high cohesion value suggests a high number of connections between group members. Modularity is a measure of the division or fragmentation within the network. Low modularity indicates that individuals of a social group are mostly interconnected with each other instead of connecting with only a subset of individuals (cluster) within the group. On the other hand, high modularity indicates that individuals are mostly connected within their own clusters instead of forming links with every individual of the social group. Related to modularity is the number of communities or clusters in the group. More cohesive networks have a low number of communities since individuals are not separated into individual clusters, but are grouped together as a whole.

Significance of the effects of fixed dominance, search radius, number of territories and the interactions among these are tested using a multi-factor ANOVA. For modularity, number of communities and cohesion, the significance is tested using a generalized linear model with a Poisson distribution and log-link.

Results

Betweenness

There is a significant effect of fixed dominance, search radius, and the interaction between these on average betweenness centralization (Table 4, Figure 1). Betweenness centralization was higher when dominance was not fixed than when it was fixed (Figure 1). Betweenness centralization increased with increasing search radius (Figure 1). The effect of fixed dominance increased with increasing search radius (Figure 1). There was not a significant effect of number of territories or its interactions on betweenness centralization.

Closeness

There is a significant effect of search radius and fixed dominance on average closeness centralization (Table 4, Figure 2). Closeness centralization increased with increasing search radius (Figure 2). Closeness centralization was higher when dominance was not fixed than when it was fixed (Figure 2). There was not a significant effect of number of territories or its interactions on closeness centralization.

Degree out

There is a significant effect of search radius, fixed dominance, and the interaction between these on average degree out centralization (Table 4, Figure 3). Degree out centralization increased with increasing search radius (Figure 3). Degree out centralization was higher when dominance was not fixed than when it was fixed (Figure 3). The effect of fixed dominance increased with increasing search radius (Figure 3). There was not a significant effect of number of territories or its interactions on degree out centralization.

Degree in

There is a significant effect of search radius, fixed dominance, and the interaction between these on average degree in centralization (Table 4, Figure 4). Degree in centralization increased with increasing search radius (Figure 4). Degree in centralization was higher when dominance was not fixed than when it was fixed (Figure 4). The effect of fixed dominance increased with increasing search radius (Figure 4). There was not a significant effect of number of territories or its interactions on degree in centralization.

Eigenvector centrality

There is a significant effect of search radius and fixed dominance on average eigenvector centralization (Table 4, Figure 5). Eigenvector centralization increased with increasing search radius (Figure 5). Eigenvector centralization was higher when dominance was not fixed than when it was fixed (Figure 5). There was not a significant effect of number of territories or its interactions on eigenvector centralization.

Linearity

There is a significant effect of search radius, fixed dominance, the interaction between search radius and fixed dominance, and the interaction between fixed dominance and number of territories on average Landau's h (a measure of linearity) (Table 4, Figure 6). H increased with increasing search radius (Figure 6). Linearity was higher when dominance was not fixed than when it was fixed (Figure 6). The effect of fixed dominance increased with increasing search radius (Figure 6). The effect of fixed dominance increased with the number of territories (Figure 6). There was not a significant effect of number of territories on h. However, the interaction between number of territories and fixed dominance had a significant effect on h.

Modularity

There is a significant effect of search radius and fixed dominance on average modularity (Table 5, Figure 7). Modularity decreased with increasing search radius (Figure 7). Modularity was higher when dominance was fixed than when it was not fixed (Figure 7). There was not a significant effect of number of territories or its interactions on modularity.

Number of communities

There is a significant effect of search radius on average number communities (Table 5, Figure 8). Number of communities decreased with increasing search radius (Figure 8). There was not a significant effect of number of territories or its interactions on the number of communities.

Cohesion

There is a significant effect of search radius and fixed dominance on average cohesion (Table 5, Figure 9). Cohesion increased with increasing search radius (Figure 9). Cohesion was higher when dominance was not fixed than when it was fixed (Figure 9). There was not a significant effect of number of territories or its interactions on cohesion.

Discussion

Linearity as measured by networks' Landau's h value was higher when dominance is not fixed compared to when it is fixed (Figure 6). Fixed dominance had a significant effect on the Landau's h value (Table 1), implying that the hierarchy is more linear when dominance is not fixed. This supported my prediction that winner-loser effects will results in more linear hierarchies. Previous research done on this subject had similar results, where winner-loser effect gave rise to more linear hierarchies (Lehner, Rutte, & Taborsky, 2011).

Having a fixed dominance resulted in higher modularity (Figure 7) and lower cohesion (Figure 9) as predicted. When dominance is fixed, winner-loser effect will not be taking place, giving rise to a less connected network. This can be explained by the fact that individuals with similar initial dominance will always fight when they encounter each other. Since fighting causes the pair to move away from each other, the chance of future interactions will be reduced, thereby reducing the connectedness of the network. Therefore, the minimum number of links to be broken to separate one node from the network is low. In a less connected network, individuals are not well connected with every member of the group, resulting in a high modularity value. On the other hand, when dominance is not fixed, winner-loser effects result in individuals' dominance values to become more different, eventually moving out of the range in which aggression is likely, allowing individuals to stay close to each other. However, fixed dominance did not have a significant effect on the number of communities. This differs from my prediction that having fixed dominance will result in a higher number of communities. A possible explanation is that when dominance is fixed, interactions between individuals are so low that even communities are not well established.

Results showed that all measures of variation in connectivity of individuals, which includes mean betweenness centralization, mean closeness centralization, mean indegree centralization, mean outdegree centralization and mean eigenvector centralization, reflected a significant effect of fixed dominance (Table 4). These measures of variation in influence are higher when dominance values are not fixed (Figure 1-5). When dominance values are subjected to change during aggressive encounters, winner-loser effects can take place, giving rise to a strong dominance hierarchy with a more connected network structure. Within the strong dominance hierarchy, some individuals are more influential than others, as supported by the high centralization values. This confirms my prediction that winner-loser effects give rise to strong dominance hierarchies with high centralization values since it allows some individuals to have more interactions compared to other individuals. Experiment done on pigs had similar results, where pigs placed in a pen with familiar individuals had higher centralization scores compared to pigs placed with foreign individuals due to the influence of winner-loser effect (Büttner, Scheffler, Czycholl, & Krieter, 2015).

Increase in search radius resulted in higher centralization (Figure 1-5), cohesiveness (Figure 7-9) and more linear dominance hierarchy (Figure 6) as predicted. In the real world, the search radius of fish is affected by factors such as clarity of water and the visual ability of the fish. This can be explained by the increase in the number of possible interactions due to an increased range of interaction, allowing individuals to have more interactions with each other. With more interactions, a strong dominance hierarchy can be established, where individuals have a greater difference in their level of influence, as reflected by a higher centralization values (Table 4). A more connected network due to an increased search radius resulted in the increase in cohesion value, thus increasing the minimum number of links to be broken to separate a single node (Figure 9). This will also lead to a lesser number of communities (Figure 8) and modularity (Figure 7) value since individuals are well connected with members of the entire group after increasing their interaction by expanding the search radius.

I also predicted that number of territories should have an effect on the group cohesiveness, connectivity and structure. However, number of territories did not have a significant effect on these network measures. My initial prediction assumes that more territories allow for more focal locations for interactions, giving rise to a strong dominance hierarchy. Results from the model did not show significant effect of number of territories, possibly because a few extremely dominant individuals settled at the territory. Dominant individuals have a preference to move towards a territory. As other individuals came across the territory, relatively subordinate individuals will lose a fight and move away from the territory. Over time, individuals who settled at the territory will have dominance values that are much higher than average. Dominance value of other individuals who came across the territory will be much lower in comparison, which does not meet the criteria for an aggressive interaction, namely similar dominance value. Thus, the interactions happening at the territory will be rather limited, failing its function as a focal location for interactions.

Further research can be done to explore possible factors that enable territories to function as focal locations for interactions. Such factors include incorporating subordinate helpers into the model. In real life, dominants and helpers benefit from each other (Wong & Balshine, 2011). This is an important characteristic of cooperative breeding *N. pulcher* that is not reflected in this model. When helper-breeder relationship is established, both subordinates and dominant individuals will inhabit the territory, possibly allowing for more interactions to take place at the territory.

This model of *N. pulcher* behavior is similar to real *N. pulcher* behavior in a way that aggression is more likely to happen between individuals of similar size and that larger individuals tend to be more aggressive (Schuerch & Heg, 2010). *N. pulcher* start their life as subordinates helping the dominant breeding pair in their territories (Wong & Balshine, 2011). However, in my model, subordinates are not attracted to the territory in any way, and they move away from one if they lose a fight.

This model, together with most previous research, assumes that social networks do not change over time (Pinter-Wollman *et al.*, 2014). A static measure of the network is conducted towards the end of each run. However, individual behaviors change over time as new social connections are formed and after a disturbance. Future research can focus on the dynamic aspect of the social network can be studied, allowing for a more realistic representation of a social network over time. Dynamic measures can be analyzed by gathering network measurements at each time step instead of only towards the end. Results of dynamic measurements can be used to predict changes in dynamic social network and give a better understanding of how conflict is managed in social groups.

Further research can also explore central, more influential individuals. Central individuals could be dominant, submissive, or have average dominance, and which individual is most central may depend on the measure of centrality. I predict that individuals with high betweenness centrality, for example, have average dominance values since their rank allows them to interact with the most number of individuals. Since individuals have a tendency of forgetting results of past interactions, they might reset their dominance value to one that reflects the average dominance. Central individuals with average dominance will be able to interact with these individuals as they reset their dominance values since they will have similar dominance. These central individuals can also be dominant individuals since they are more aggressive and have a greater chance of initiating fights than do more subordinate individuals. Mid-ranking individuals stay in territories of dominant individuals, which allow them to be exposed to both the dominant individuals and more subordinate individuals, making it possible for them to be the central individuals. Exploring whether and how centrality measures are related to rank will be important for understanding my centralization results.

This research concluded that winner-loser effect allowed for the establishment of a strong dominance hierarchies with high variation in connectivity and cohesion. Ability to detect other fish in the social network also had a significant effect on the establishment of strong dominance hierarchies by allowing for more interactions within the social group. Territories did not serve as focal sites for interactions possibly due to the establishment of highly ranked individuals on site, limiting the number of possible aggressive interactions with other members of the group.

Social network models such as the one in this study are useful because they can provide important insights to the evolution of social behavior. Since this is a simple model of key behaviors of social fish, it can be used to reflect the earlier stages of the evolution from solitary fish to social groups. Other models that incorporated a wider range of more complex behaviors reflect the later stages of evolution. By comparing the results from more complex models and simpler models, the evolution of social behavior can be outlined. This will in turn give us insights of how network structures evolved to be more complex and how individuals benefit the social group as a whole, while balancing the cost associated with group living.

Acknowledgement

I thank my project advisor, Ian Hamilton for guiding me through this research and for meaningful discussions surrounding network analysis. I also thank Sui Chian Phang who helped me to develop R scripts.

Appendix

Table 1 Agent state variables used in the model

Variable	**Description**
Dominance level of individuals	Each individual is assigned a random dominance value of between 20 to 80 at the start of each run. Dominance influences the outcome of fights and, depending on other model variables, how fights occur.
Sex of individuals	Individuals are assigned either male or female, since aggression is sex based
Location	Individuals and territories are placed in random coordinates in the world
Links to	Aggression from the individual towards a target
Links from	Aggression from an aggressor towards the individual

Table 2 Environment state variables used in the model.

Variable	**Description**
Search radius	Targets and territories will only be selected if they fall within the search radius
Number of individuals	Number of females and males can be varied independently
Number of territories	Number of territories can be varied
Fixed dominance	Turning on this switch will disallow individuals' dominance values to be altered after an aggressive interaction. This switch allows running the model with or without winner-loser effects

Table 3 Initialization values used in the model

Variables	**Values**
Search radius	3, 6 or 9
Number of individuals	5, 10, or 15 for each sex
Number of territories	1, 2, 3
Fixed dominance	Yes or no.

Table 4 Summaries of ANOVA results for centralization. Only significant effects are shown. All models included search radius, fixed dominance and number of territories and all interactions among these.

Variable	Factor(s)	F value	$Df_{numerator}$	$Df_{denominator}$	P value
Betweenness	Search radius	53.360	2	341	<0.001
	Fixed dominance	13.240	1		<0.001
	Search radius * fixed dominance	10.106	2		<0.001
Closeness	Search radius	113.803	2		<0.001
	Fixed dominance	5.801	1		<0.05
Degree out	Search radius	20.688	2		<0.001
	Fixed dominance	46.711	1		<0.001
	Search radius * fixed dominance	4.623	2		<0.05
Degree in	Search radius	33.701	2		<0.001
	Fixed dominance	65.101	1		<0.001
	Search radius * fixed dominance	7.468	2		<0.001
Eigenvector	Search radius	192.701	2		<0.001
	Fixed dominance	14.982	1		<0.001
Devries	Search radius	60.835	2		<0.001
	Fixed dominance	26.307	1		<0.001
	Search radius * fixed dominance	58.991	2		<0.001
	Fixed dominance * number of territories	3.367	2		<0.05

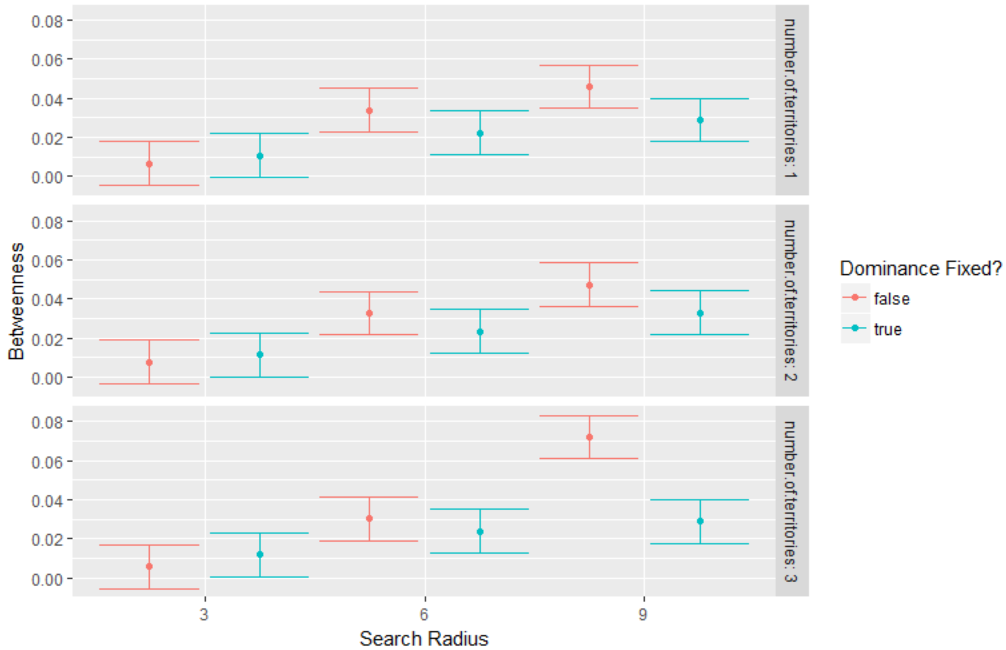

Figure 1 Effects of model parameters on betweenness centralization. X-axis represents the search radius while the y-axis represents the average betweenness centralization values. Values in blue represents fixed dominance while values in red represents non-fixed dominance. Panels represents the various number of territories

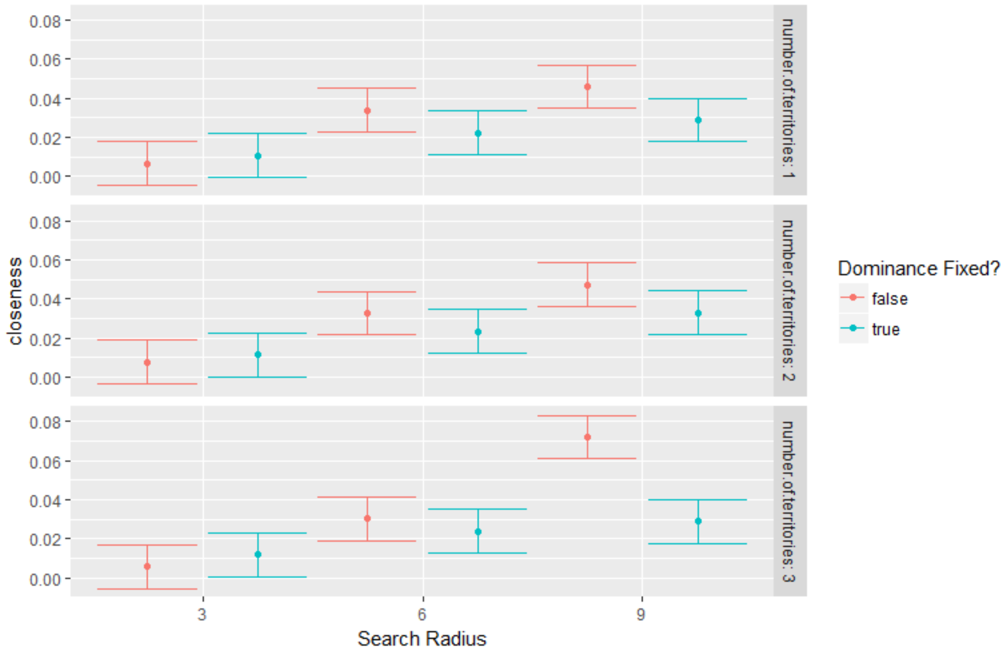

Figure 2 Effects of model parameters on closeness centralization. X-axis represents the search radius while the y-axis represents the average closeness centralization values. Values in blue represents fixed dominance while values in red represents non-fixed dominance. Panels represents the various number of territories

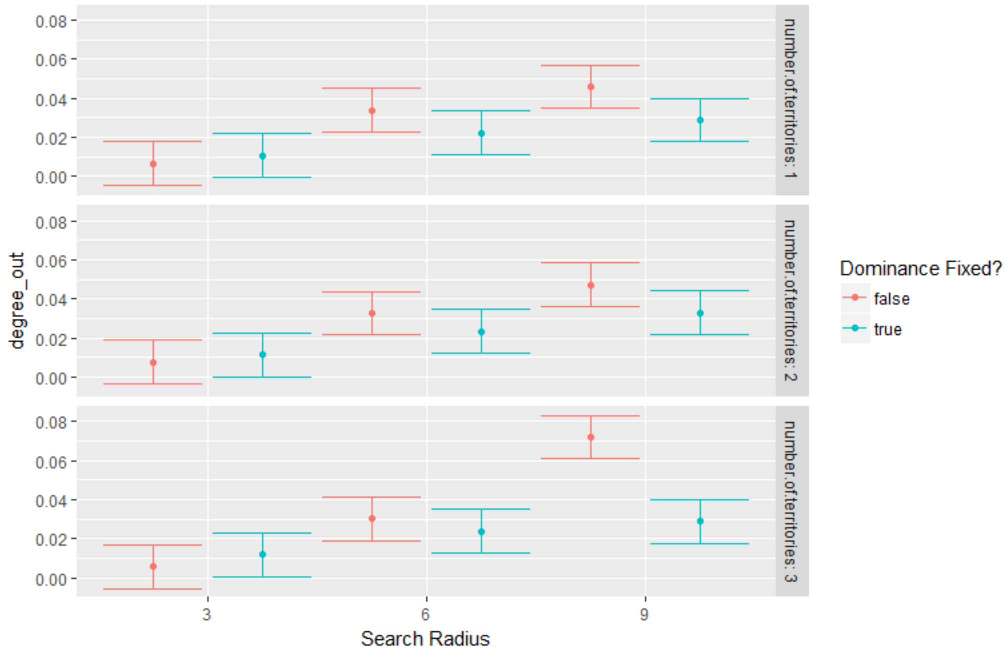

Figure 3 Effects of model parameters on degree out centralization. X-axis represents the search radius while the y-axis represents the average degree out centralization values. Values in blue represents fixed dominance while values in red represents non-fixed dominance. Panels represents the various number of territories

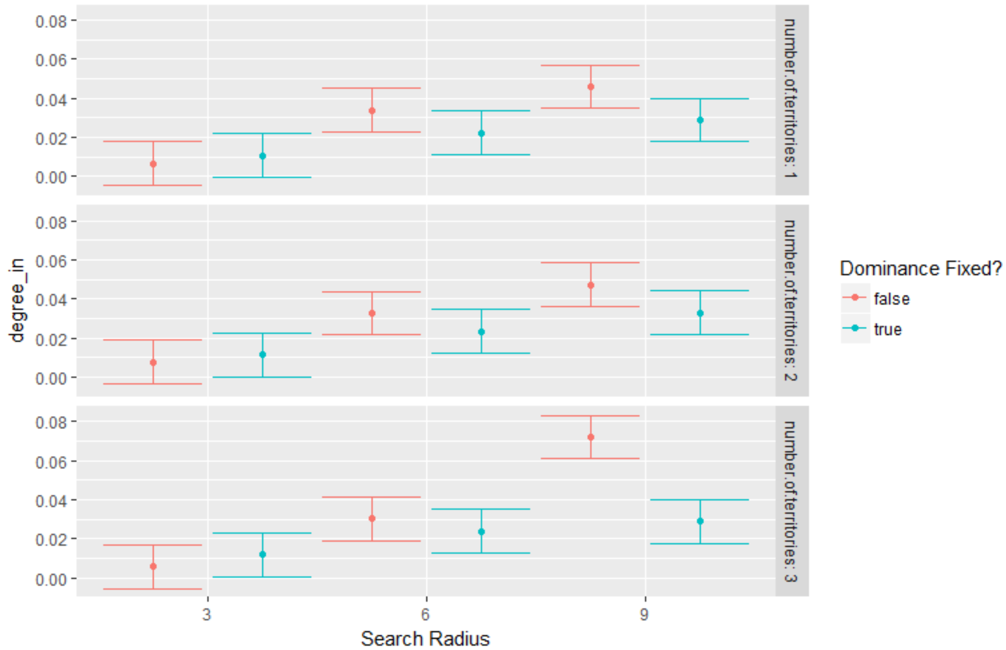

Figure 4 Effects of model parameters on betweenness degree in. X-axis represents the search radius while the y-axis represents the average degree in centralization values. Values in blue represents fixed dominance while values in red represents non-fixed dominance. Panels represents the various number of territories

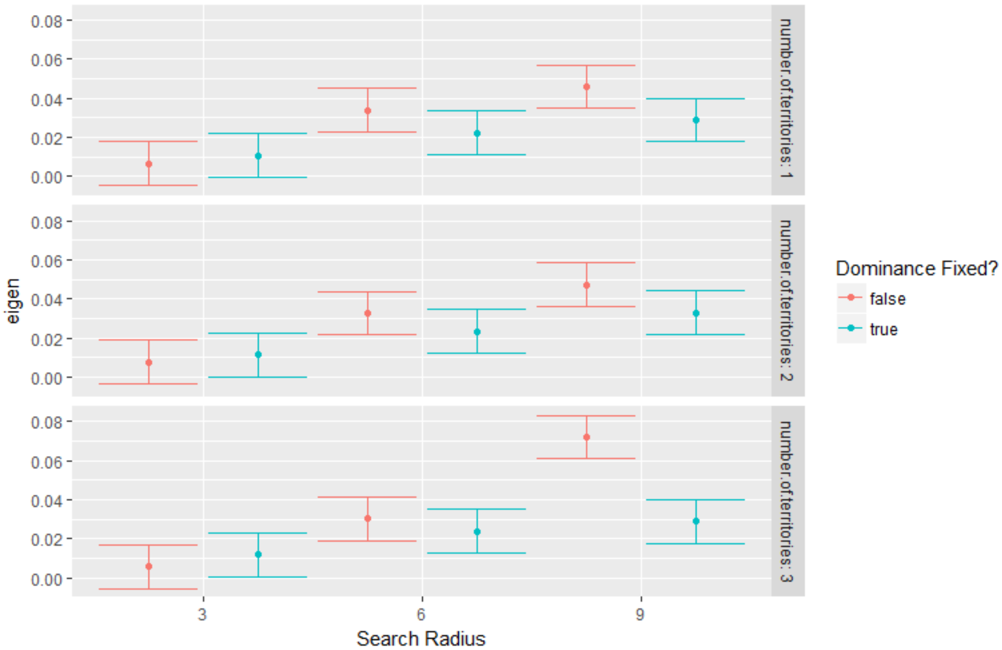

Figure 5 Effects of model parameters on eigenvector centralization. X-axis represents the search radius while the y-axis represents the average eigenvector centralization. Values in blue represents fixed dominance while values in red represents non-fixed dominance. Panels represents the various number of territories

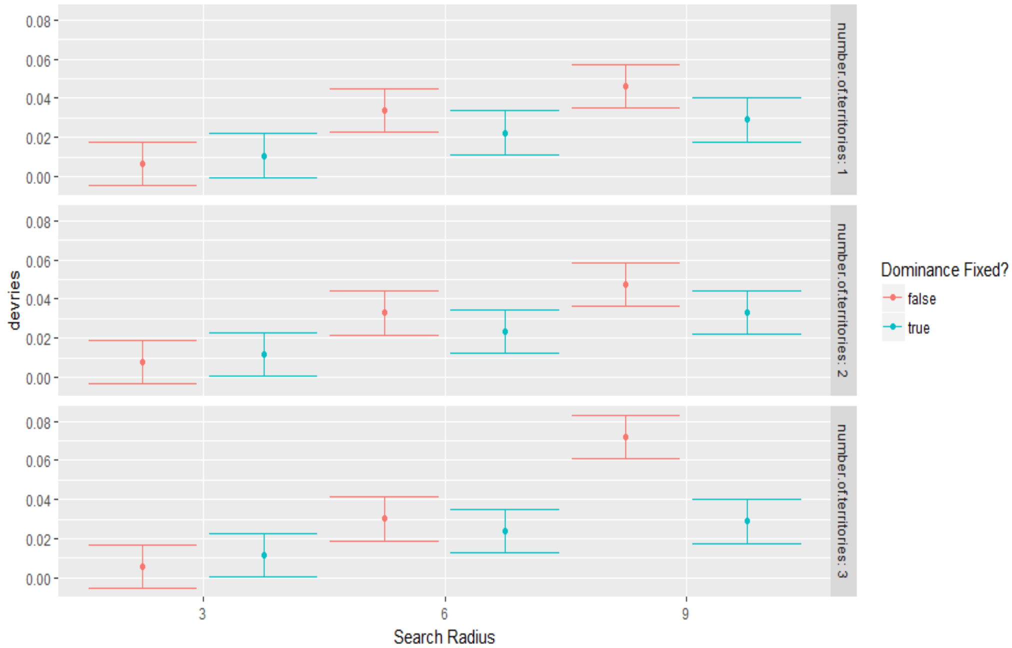

Figure 6 Effects of model parameters on linearity. X-axis represents the search radius while the y-axis represents the average h values. Values in blue represents fixed dominance while values in red represents non-fixed dominance. Panels represents the various number of territories

Table 5 Summaries of GLM results for centralization. Only significant effects are shown. All models included search radius, fixed dominance and number of territories and all interactions among these.

Variable	Factors	χ^2	Df	P value
modularity	Search radius	948.60	2	<0.001
	Fixed dominance	33.81	1	<0.001
Number of communities	Search radius	14.5032	2	<0.001
Cohesion	Search radius	11.5137	1	<0.001
	Fixed dominance	9.0574	1	<0.01

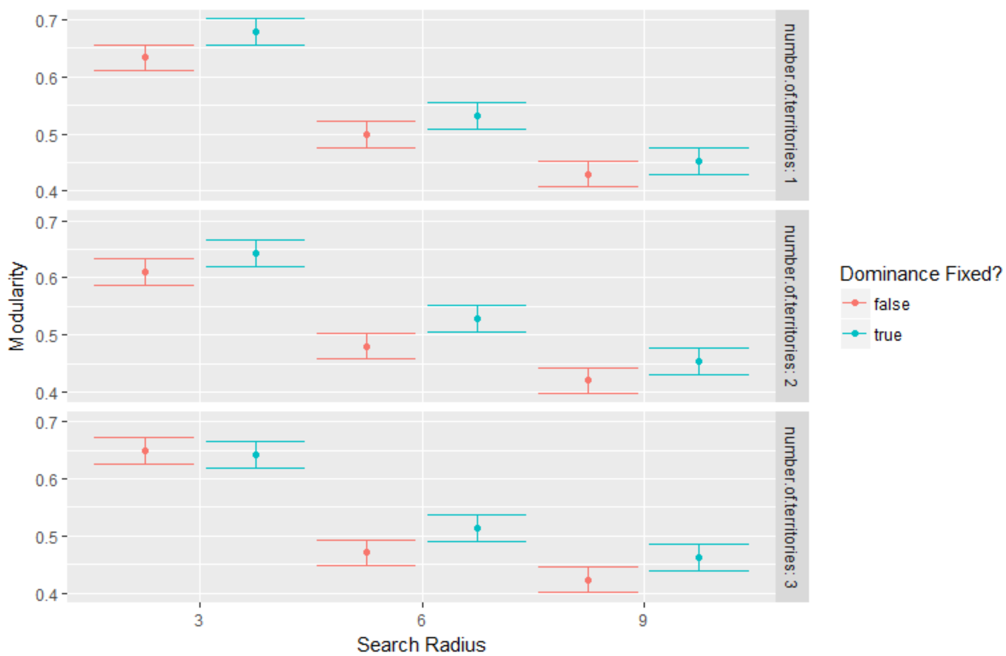

Figure 7 Effects of model parameters on modularity. X-axis represents the search radius while the y-axis represents the average modularity vlaues. Values in blue represents fixed dominance while values in red represents non-fixed dominance. Panels represents the various number of territories

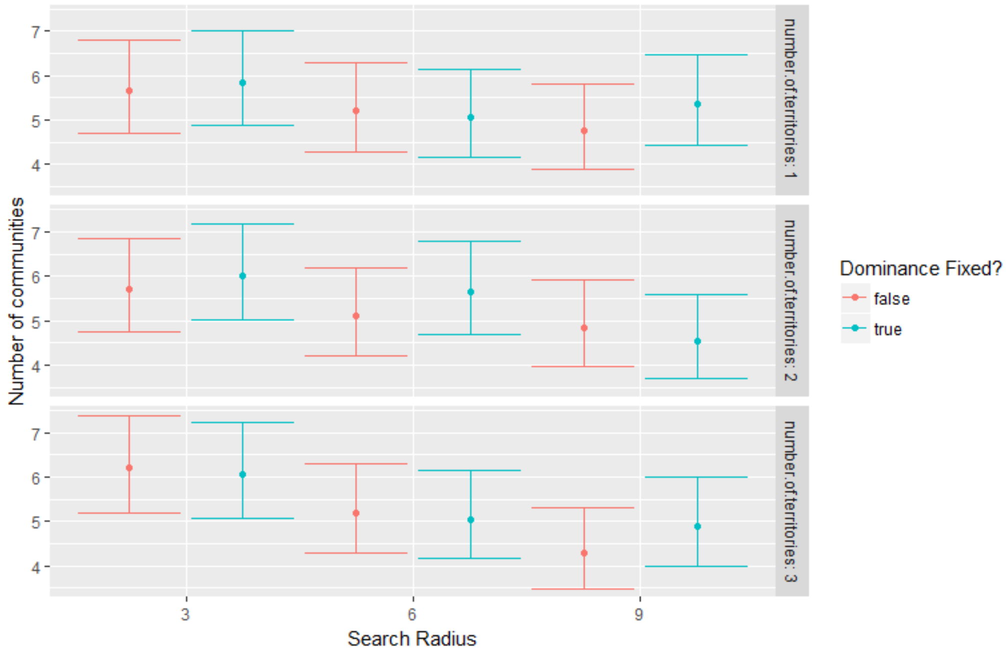

Figure 8 Effects of model parameters on number of communities. X-axis represents the search radius while the y-axis represents the average number of communities. Values in blue represents fixed dominance while values in red represents non-fixed dominance. Panels represents the various number of territories

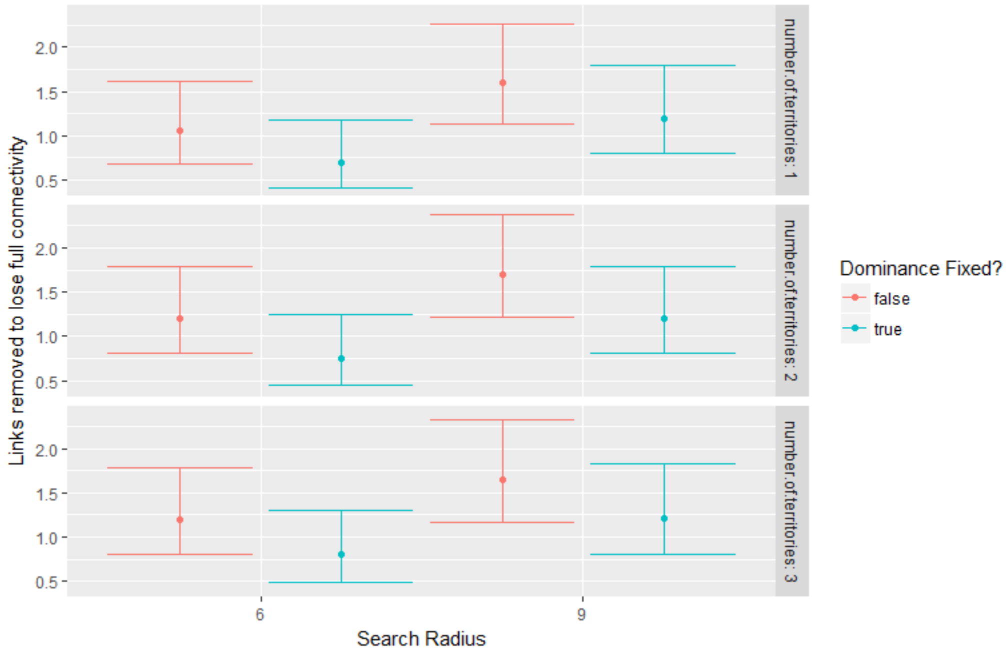

Figure 9 Effects of model parameters on cohesion. X-axis represents the search radius while the y-axis represents the average cohesion values. Values in blue represents fixed dominance while values in red represents non-fixed dominance. Panels represents the various number of territories

References

Abell, J., Kirzinger, M. W., Gordon, Y., Kirk, J., Kokeŝ, R., Lynas, K., Mandinyenya, B., ... Youldon, D. (2013). A social network analysis of social cohesion in a constructed pride: implications for ex situ reintroduction of the African lion (Panthera leo). *Plos One, 8,* 12.

Baglione, V., Marcos, J. M., Canestrari, D., & Ekman, J. (2002). Direct fitness benefits of group living in a complex cooperative society of carrion crows, Corvus corone corone. *Animal Behaviour, 64,* 6, 887-893.

Beauchamp, G. (2014). *Social predation: How group living benefits predators and prey*. (*135-156*)

Büttner, K., Scheffler, K., Czycholl, I., & Krieter, J. (2015). Social network analysis - centrality parameters and individual network positions of agonistic behavior in pigs over three different age levels. *Springerplus, 4,* 1, 1-13.

Clutton-Brock, T. H., Gaynor, D., McIlrath, G. M., Maccoll, A. D. C., Kansky, R., Chadwick, P., Manser, M., ... Brotherton, P. N. M. (1999). Predation, group size and mortality in a cooperative mongoose. *Journal of Animal Ecology, 68,* 4, 672-683.

De Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour, 50,* 5.

Godoy, I., Vigilant, L., & Perry, S. E. (2016). Inbreeding risk, avoidance and costs in a group-living primate. *Behavioral Ecology and Sociobiology, 70,* 9, 1601-1611.

Goessmann, C., Hemelrijk, C., & Huber, R. (2000). The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties. *Behavioral Ecology and Sociobiology, 48,* 6, 418-428.

Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., & Railsback, S. F. (2010). The ODD protocol: A review and first update. *Ecological Modelling, 221,* 23, 2760-2768.

Lehner, S. R., Rutte, C., & Taborsky, M. (2011). Rats Benefit from Winner and Loser Effects. *Ethology, 117,* 11, 949-960.

Moosa, M. M & Ud-Dean, S. M. M. (2011). The Role of Dominance Hierarchy in the Evolution of Social Species. *Journal for the Theory of Social Behaviour, 41,* 2, 203-208.

Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de, S. S., Waters, J. S., ... McDonald, D. B. (2014). The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behavioral Ecology, 25,* 2, 242-255.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Rypstra, A. L. (1993). Prey size, social competition and the development of reproductive division of labor in social spider groups. *The American Naturalist, 142,* 5.

Schuerch, R., & Heg, D. (2010). Life history and behavioral type in the highly social cichlid Neolamprologus pulcher. *Behavioral Ecology, 21,* 3, 588-598.

Schradin, C., König, B., & Pillay, N. (2010). Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *Journal of Animal Ecology, 79*, 3, 515-521.

Schwartzer, J. J., Ricci, L. A., & Melloni, R. H. (2013). Prior Fighting Experience Increases Aggression in Syrian Hamsters: Implications for a Role of Dopamine in the Winner Effect. *Aggressive Behavior, 39,* 4, 290-300.

Stephens, P. A., Russell, A. F., Young, A. J., Sutherland, W. J., Clutton-Brock, T. H., & Associate, E. N. P. (2005). Dispersal, Eviction, and Conflict in Meerkats (Suricata suricatta): An Evolutionarily Stable Strategy Model. *The American Naturalist, 165,* 1, 120-135.

Sueur C, Deneubourg JL, Petit O, Couzin ID (2011) Group size, grooming and fission in primates: A modeling approach based on group structure. J Theor Biol 273: 156–166

Sueur, C., & Maire, A. (2014). Modelling animal group fission using social network dynamics. *Plos One, 9,* 5.

Thompson, F. J., Donaldson, L., Johnstone, R. A., Field, J., & Cant, M. A. (2014). Dominant aggression as a deterrent signal in paper wasps. *Behavioral Ecology, 25, 4, 706–715.*

West-Eberhard, M. J. (1979). Sexual Selection, Social Competition, and Evolution. *Proceedings of the American Philosophical Society, 123,* 4, 222-234.

Wilensky, U. (1999). NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

Wong, M., & Balshine, S. (2011). The evolution of cooperative breeding in the African cichlid fish, Neolamprologus pulcher. *Biological Reviews, 86,* 2, 511-530.